Biodiversity, community structure and function of biofilms in stream ecosystems

Katharina Besemer[a,b,]*

[a]) School of Engineering, University of Glasgow, Rankine Building, Oakfield Avenue, Glasgow G12 8LT, United Kingdom

[b]) Department of Limnology and Bio-Oceanography, University of Vienna, Vienna Ecology Center, Althanstraße 14, A-1090 Vienna, Austria

katharina.besemer@univie.ac.at *Correspondence and reprints

Abstract

Multi-species, surface-attached biofilms often dominate microbial life in aquatic environments where they contribute substantially to biogeochemical processes. The microbial diversity of natural biofilms is huge, and may have important implications for the functioning of aquatic ecosystems and the services they provide. Yet the causes and consequences of biofilm biodiversity remain insufficiently understood. This review aims to give an overview of current knowledge on the distribution of biofilm biodiversity, the mechanisms generating biodiversity patterns and the relationship between biofilm biodiversity and ecosystem functioning.

Keywords

biofilm; microbial diversity; microbial ecology;

Introduction

In natural aquatic environments, microbial cells are often found in complex, surface-attached communities, known as biofilms [1,2]. Microbial biofilms dominate biogeochemical processes in many sedimentary environments, such as stream and riverbeds, lake sediments or groundwater aquifers [3,4]. The attachment to a surface extends the residence time of microorganisms relative to the transport of water and solutes and enhances the potential for metabolism of substrates [3]. Further, the stable juxtaposition of microbial cells renders biofilms coordinated functional consortia, which makes them more efficient than mixed communities of planktonic cells [1,2]. The resulting complex network of interactions, a surprising level of multi-cellular behavior and extensive three-dimensional structures act in concert to create the taxonomic and functional diversity which characterizes biofilms [1,2].

Biofilms develop in virtually every interfacial environment [2,3] and on a wide variety of organic and inorganic substrates, the nature of which has important implications for their structure and function [5]. The rocks, cobbles and sand constituting stream- and riverbeds or groundwater aquifers offer a large surface area for colonization by epilithic (on stones) and epipsammic (attached to sand grains) biofilms [6,7]. In fine sediments, such as in lakes, floodplains and marshes, biofilms can form a cohesive matrix closely surrounding and embedding sediment particles, which can have an important role in stabilizing sediments against re-suspension [8]. Plant-associated (epiphytic) biofilms may have beneficial or harmful effects on the host, and biofilms on submerged wood (epixylic) and leafs are prominent players in organic matter re-mineralization [9,10]. Furthermore, microbial assemblages associated with suspended detrital aggregates can be regarded as “mobile biofilms”, a microbial lifestyle analogous to an attached biofilm but acclimated to a different hydrodynamic regime and available surface area [3]. Benthic

(the interface between stream water and sediment) and hyporheic (the sedimentary interface where streamwater and groundwater mix) biofilms typically dominate microbial life in ecosystems with large sediment-surface-area to water-volume ratios, such as streams [3,6,7], while biofilms on submerged plants or attached to suspended aggregates are of major importance in larger rivers, estuaries and lakes [10,11]. The nature of the substratum (chemical composition, surface area, stability) colonized by the biofilm microbiota has important consequences for biofilm structure and function and differentiates biofilm communities among habitats even within the same environment [10,12–14]. The biodiversity of natural biofilms will eventually determine the metabolic performance of these communities, and thereby the functioning of aquatic systems and the ecosystem services they provide [15,16].

In this review, I aim to give an overview of findings on the distribution of microbial diversity of natural biofilms, the mechanisms generating biodiversity patterns and the relationship between biofilm biodiversity and ecosystem functioning. While the focus of this review lies on the prokaryotic diversity of biofilms in the benthic and hyporheic zone of streams and rivers, I include some examples from other environments and from eukaryotic organisms to give a more comprehensive picture.

Biofilm biodiversity and distribution patterns

Biofilms harbor considerable microbial diversity. Bacteria, archaea, algae, fungi, protozoa and viruses all form important components of the biofilm matrix and contribute to the biodiversity and ecosystem processes of aquatic ecosystems [2,13,17]. The most prominent bacterial groups in freshwater biofilms are typically *Proteobacteria*, *Bacteroidetes* and cyanobacteria [5]. Particularly, *Beta-Proteobacteria* often dominate biofilms in streams, rivers and on lake aggregates [7,11,18,19], which agrees with findings for the respective planktonic communities

[20]. However, *Alpha-Proteobacteria*, which are typically numerically dominant in marine ecosystems [20], can be as abundant – or even more abundant – than *Beta-Proteobacteria* in freshwater biofilms, ranging from epilithic and hyporheic stream biofilms [21–24] to biofilms on living or decaying plants [10], and to diatom-aggregates in lakes [25]. The ability to degrade humic substances and a tendency to form grazing-resistant morphologies may favor certain members of *Alpha-Proteobacteria* in freshwater biofilms [20]. The capability to use complex macromolecules might also be responsible for the high abundance of *Bacteroidetes* in many freshwater biofilm communities [21,26] and particularly in aggregate-associated communities [11,25]. *Bacteroidetes* has been proposed to play an important role in the degradation of suspended particles [20], especially when labile organic compounds are already depleted and the particle increasingly consists of refractory organic material [25]. Biofilms exposed to light often contain considerable numbers of cyanobacteria [24,27]. Further taxonomic groups typically present in biofilms include *Acidobacteria* (especially at low pH; [28]), *Actinobacteria*, *Firmicutes*, *Gemmatimonadetes*, *Gamma-* and *Delta-Proteobacteria*, *Verrucomicrobia*, *Planctomycetes*, and *Deinococcus-Thermus* [18,23,24,26,27].

Archaea have repeatedly been found to be of minor importance for stream- and river-biofilms [12,23], though some exceptions have been reported (relative abundances of up to 10%; [7,19]). For instance, methanogenic archaea can be a numerically prominent component (>10% relative abundance) of the hyporheic microbial community [29]. Microbial eukaryotes are an abundant and functionally important element of biofilms [30,31]. Algae, most commonly *Bacillariophyta* and *Chlorophyta*, provide substrates by exudates and lysis products and are a major carbon source for heterotrophic biofilm microbes [7,32]. Fungi, especially *Ascomycota*, can be a prominent structuring element of biofilms and play an important role in the decomposition of submerged organic matter [9,33]. Lastly, protists (including flagellates, ciliates, and amoebae)

89 and viruses can control biofilm growth and alter biofilm diversity, architecture and function
90 [17,30].

91 The diversity and composition of biological communities are shaped by the interplay of regional
92 (dispersal dynamics, landscape patterns) and local (abiotic habitat conditions, biotic interactions)
93 processes [34] (Figure 1). The role of regional processes for microbial communities is the subject
94 of ongoing debate. High dispersal rates and short generation times have been proposed to render
95 geographical distances less important than environmental factors for microbial biodiversity
96 patterns [28,35]. Indeed, stochastic immigration from the source community suspended in the
97 overlying water column into the biofilm was insufficient to explain microbial community
98 composition in boreal [18] and glacier-fed stream biofilms [36], suggesting that the local
99 environment and biotic interactions select microorganisms from the stream water for biofilm
100 formation. Consistently, Fierer and colleagues [28] found that pH, dissolved organic carbon and
101 nitrogen could predict most of the variation between bacterial communities inhabiting fine
102 benthic organic matter in streams, while no evidence was found for an effect of geographic
103 distance *per se*. Furthermore, selection according to environmental conditions often prevails over
104 dispersal dynamics in shaping microbial communities in groundwater aquifers [4]. However,
105 combined effects of dispersal limitations and niche-based processes explained community
106 composition and diversity of epilithic streams biofilms across New Zealand, though the influence
107 of environmental factors was clearly stronger [37]. This agrees with findings from a study
108 comparing microbial communities from, amongst others, stream biofilms and lake sediments,
109 which reported that – while microbial community composition was primarily governed by
110 environmental processes – dispersal also played a role [38]. In a study assessing the importance
111 of dispersal for biofilm diversity at the scale of a stream network, we found that beta-diversity
112 among headwaters was higher than between larger streams [39]. This higher beta-diversity could

not be explained exclusively by the larger geographical distance – and consequently a wider range of environmental conditions – encompassed by headwaters, evoking dispersal limitation as a driver of community variation among stream biofilms in fluvial networks [5,39].

Water flow, turbulence and the landscape topography of the substratum affect microbial dispersal and colonization patterns, but also generate microhabitats that differ in shear stress and mass transfer [13,40]. Experimenting with stream mesocosms containing streambed landscapes as induced by bedforms, biofilm community composition was found to be related to the spatial variation of hydrodynamic conditions, resulting in a gradient of beta-diversity that increased with habitat heterogeneity at the landscape scale [31]. Using the same experimental setup, Woodcock and colleagues [40] showed that a neutral model of flow-induced dispersal provided a reasonable explanation for the spatial variation of biofilm community composition along streambed landscapes under a homogenous hydrodynamic regime, that is, when the streambed landscape was flat. However, stochastic immigration as the driving force of community composition failed to explain the complexity of biofilm compositional patterns in a heterogeneous flow landscape, suggesting environmental filtering of biofilm taxa [40]. This agrees with a conceptual model by Wang and colleagues [38], which proposed that dispersal limitations govern microbial community composition when the selective strength of local habitat conditions is low, as can be expected for the case of the homogenous streambed landscape.

Collectively, these findings indicate that environmental filtering is a strong driver of biofilm biodiversity patterns. The attachment to a stable surface and the increased residence time compared to free living microbes may render biofilms more susceptible to the ambient environmental conditions [31]. This notwithstanding, dispersal dynamics appear to play a role for biofilm community assembly across a range of scales (Figure 1). However, disentangling

dispersal and environmental processes as drivers of community composition is complicated by the fact that their relative importance changes not only across scales, but also during biofilm succession [13,14]. Furthermore, while common microbial taxa may be widely dispersed, rare taxa may experience dispersal constraints simply because their rarity limits the probability of successfully dispersing to new substrates [14]. Therefore, as pointed out by Fierer [35], the debate on the importance of dispersal is unlikely to be resolved any time soon as data on the actual rates of microbial dispersal are limited and difficult to obtain.

A broad range of environmental factors was identified as potential drivers of biofilm community composition and diversity (including nutrients, dissolved organic carbon, pH, temperature, hydrodynamic parameters and pollutants), of which only a few can be discussed here (see Table 1 for a summary). Water temperature, for instance, was found to correlate with the diversity and community structure of benthic [21,27,36,41,42] and hyporheic [43,44] river biofilms, and has been proposed to be the driving force for stream biofilm community variation along an altitudinal gradient [24]. Furthermore, beta-diversity among glacier-fed streams decreased with increasing stream water temperature [36]. Experimental studies found that moderate changes of water temperature (2-3°C) induced shifts in the total bacterial [23,45] and denitrifying [46] community structure in river biofilms. Changes of water temperature in this range can be expected for streams and rivers as a result of climate change, with potential consequences for biofilm structure and function. However, the specific effect of temperature for the biofilm community might be modified by interaction with other environmental variables, such as nutrients [41], or vary with successional state [45].

Streamwater pH integrates a number of environmental factors including catchment geology and hydrology, and may have direct or indirect influence on biofilm communities [28,36]. Notably,

pH was found to correlate with microbial community composition in benthic [12,21,36] and hyporheic [43] stream biofilms and was the most important variable explaining the structure of microbial communities associated with river sediments [47] and fine benthic organic matter [28]. Furthermore, pH was related to the composition of fungal and bacterial communities on decaying leafs, and the bacterial diversity of these communities was found to decrease with increasing pH [33]. In contrast, the diversity of epilithic biofilms in streams ranging from relatively pristine to highly impacted by acid mine drainage decreased with increasing acidity [22]. A number of bacterial phyla were reported to respond to changes in pH. Particularly, *Acidobacteria* were found to increase in relative abundance with decreasing pH in benthic organic matter [28] and in benthic biofilms of glacier-fed streams [36], which is plausible as this phylum is usually related to environments with low pH. Furthermore, *Proteobacteria* and the *Cytophaga-Flavobacter* group were found to increase with increasing pH, while *Gemmatimonadetes* were found to decrease with increasing pH [28, 36, 43,47].

Organic carbon and nutrients, as a prerequisite for biofilm growth, can alter the architecture, community composition and biodiversity of biofilms [2,13], but the specific mechanisms are not yet clear. Higher resource availability might reduce interspecific competition, which would support a higher diversity [48]. On the other hand, an increase in a limiting resource might favor dominance of one or a few species, thereby leading to a decline in species richness [49]. In fact, bacterial diversity in tropical stream biofilms increased with nitrate concentrations [48]. In contrast, benthic biofilm diversity was lower in a highly impacted, nutrient rich urban stream than in more pristine streams [50], while similar bacterial richness was observed in benthic biofilms along a river irrespective of nitrogen and phosphorus loads [51]. Furthermore, the structure of the fungal and bacterial communities on decaying leafs was related to phosphorus in the streamwater [33] and the stoichiometry of stream water solutes, especially the ratio of dissolved inorganic

nitrogen to soluble reactive phosphorus, explained the abundance of *Beta-Proteobacteria* and the *Cytophaga-Flavobacter* group in stream biofilms [42]. This agrees with findings from experimental stream biofilms, which showed that bacterial community composition responded to nutrient enrichments [19]. Similar findings were reported for dissolved organic carbon concentration, which was observed to explain the temporal variations in community composition of epilithic biofilms [27] and the spatial variation of the active communities of epipsammic biofilms [12]. A study in aquifers showed that overall microbial diversity decreased with increasing organic carbon concentrations, while the abundance of *Beta-* and *Gamma-Proteobacteria* increased [52]. Furthermore, an experimental study in which hyporheic biofilms were amended with a range of organic carbon substrates ranging from simple to complex and from labile to recalcitrant demonstrated the importance of organic carbon quality for biofilm community composition [53].

The availability of light, and therefore the presence of phototrophic primary producers within a biofilm has important implications for the organic carbon supply of heterotrophic biofilm microbes [32]. The close physical proximity of primary producers and heterotrophic microorganisms in biofilms may promote the rapid utilization of labile organic carbon from algal exudates by microbial cells, while dark-grown biofilms, as in the hyporheic zone for instance, rely primarily on external carbon sources [32]. This was substantiated by a field study on river biofilms, which showed that biofilms exposed to light exhibited significant internal cycling of high-quality organic carbon, while dark-grown biofilms were more dependent on the organic matter input from the water column and more efficient in using labile components [32]. Algal exudates of labile organic compounds may even enhance microbial degradation of more recalcitrant organic matter through priming or co-metabolism [3,54]. Evidence for a priming effect in aquatic systems was provided by research on biofilms growing on decaying leafs, which

showed that the presence of diatoms increased leaf litter decomposition rates [54]. Furthermore, increased quality and diversity of organic carbon through algal exudates may support microbial biodiversity [55], as reported for bacteria in benthic biofilms [32] and fungi in mixed-species biofilms on leaf litter [54]. However, a slightly negative [56] or no consistent effect [23] of light availability on microbial diversity was observed in experimental stream biofilms. Competition for inorganic nutrients or allelopathic compounds produced by algae and cyanobacteria might be responsible for a negative effect of primary producers on the diversity of heterotrophic microorganisms [54]. This is indeed supported by a study on benthic stream biofilms, which found a negative relationship between the relative abundance of cyanobacteria and overall microbial diversity [39].

From biofilm biodiversity to ecosystem functioning

The relationship between diversity, community composition and ecosystem processes is a key issue of ecology [15] and is gaining increasing interest in microbial ecology. Numerous studies indicated that diversity influences productivity and *vice versa* but the shape of this relationship and the underlying mechanisms remain debated [16]. Complementarity effects, such as niche partitioning or facilitation, are assumed to increase the performance of the community above the level expected by the performance of the individual contributing species [15]. However, a positive diversity-function relationship can also arise from purely stochastic sampling effects, because more diverse communities have a higher probability of containing highly productive species [15]. In this case, the community composition and functional identity is more important than species diversity *per se* [16]. The proximity of various microbial taxa and small-scale spatial variation in biofilm architecture may foster functional complementarity in biofilms [1,57]. Indeed, an experimental study on stream biofilms indicated that complementarity effects

contributed to resource uptake patterns in mesocosms differing in physical heterogeneity [57]. Community variation along streambed landscapes, dissolved organic carbon uptake, and the molecular diversity of used organic compounds all increased with increasing flow heterogeneity. This suggests that the biofilm differentiated into functionally non-redundant local communities, whose diversified metabolic capabilities then induced complementarity at the regional scale [57]. Similarly, niche complementarity among species was shown to enhance biofilm biomass and nitrogen uptake in algal biofilms grown in heterogeneous flow environments [58]. This study indicated that more diverse communities were able to take greater advantage of the niche opportunities provided by the environment, which enabled the biofilms to capture a greater proportion of the available resources. When these niche opportunities were experimentally removed by making the flow environment homogenous, species-specific selection effects were responsible for higher biomass in more diverse communities [58]. These findings suggest that diversity and functional complementarity might be important mechanisms supporting the functioning of natural biofilm communities.

Both biofilm community structure and function have been shown to respond to environmental forcing, but to what extent changes in functioning are mediated by changes in community structure remains elusive as yet [28,31,53]. The structure-function relationship of a community can be modified by functional redundancy, which implies that different taxa have similar functional roles in a community, and by metabolic plasticity, which is the capacity of a community to respond to environmental forcing by adjusting the metabolic performance of existing taxa [59]. The relative importance of functional redundancy and metabolic plasticity may change with environmental context [44,59], which may in part explain the contradictory patterns observed in natural biofilms. For instance, shifts in community composition were found to parallel shifts in mineralization rates of fine benthic organic matter, suggesting direct or indirect

linkages between microbial community composition and function in streams [28]. In contrast, a disconnect between community structure and function was found for bacterial communities in stream sediments, where enzymatic activity showed pronounced seasonal changes, whereas community composition exhibited no temporal pattern [60]. Weak coupling between community structure and metabolic activity and sharper distinctions between functional than between compositional patterns were observed in hyporheic stream biofilms, suggesting that the biofilm function responded faster to environmental change than community composition [61]. In an experimental study, variations in resource supply drove changes in both community composition and functional capacity of hyporheic biofilms, while no significant effect of the initial community composition on function was detected [53]. These authors suggested that the high abundances of bacteria, many of which are not actively metabolizing, constitute a reservoir of diversity in natural biofilm communities providing the genetic capability to respond to changes of environmental conditions [53]. Another experimental study on hyporheic stream biofilms found that neither community structure nor function showed clear responses on carbon and nutrient amendments, indicative of a certain level of functional redundancy [62]. However, the composition of the active microbial community and enzymatic activity were correlated as both changed over time, while no such correlation was detected for the bulk microbial community [62]. This supports the notion that biofilm activity and metabolic performance adapt rapidly to current environmental conditions, while the bulk community composition might reflect an integrated response over some previous time interval [61]. Recently, it has been recognized that complementarity across multiple functions might be necessary to maintain overall ecosystem functioning, even when single functions appear well buffered by functional redundancy in a community [63]. Indeed, the likelihood of sustaining multi-functionality in freshwater biofilms

measured as the activity of several extracellular enzymes was found to decrease with decreasing diversity, indicating a limited level of functional redundancy [64].

The degree of multi-functionality and functional redundancy of a community may in part depend on the distribution of generalist or specialist taxa within each functional group [65]. One might hypothesize that specialist taxa are favored in biofilms because of the stable juxtaposition of microbial cells with complementary metabolic capabilities [1]. However, generalist taxa may contribute more to multifunctional redundancy, owing to their metabolic plasticity [65]. Addressing the interplay between microbial diversity, multi-functionality and the distribution of ecological strategies along an altitudinal gradient, a study on benthic stream biofilms found that diversity and specialization decreased with altitude, possibly following a gradient of resource diversity [66]. Multifunctional redundancy was generally high, owing to the high abundance of apparent generalist species along the investigated altitudinal gradient [66]. Another study also found that generalist taxa were distributed throughout the whole river continuum, but indicated an elevated number of specialist taxa at the most upstream site, potentially caused by more extreme pH conditions at this site [21]. A general prevalence of generalist taxa was also reported for biofilms on decomposing leafs in streams [9]. Environmental dynamics may influence the strategy with which biofilm communities adapt to local change, as indicated for hyporheic biofilms in glacier-fed and groundwater-fed streams. While biofilms in glacier-fed streams exhibited a strong link between structure and function indicating a major prevalence of specialists, biofilms in groundwater-fed streams appeared to be dominated by generalists, which adapted to environmental dynamics by changing their metabolism [44].

As the relationship between taxonomic diversity and the diversity of functional groups can be modified by the degree of functional redundancy in a community, functional diversity has

repeatedly been suggested to be a more suitable predictor of ecosystem processes [16]. Several studies addressed the importance of functional diversity in biofilms and their responses to environmental conditions such as drought events and rising temperatures, as they are likely to occur as a result of human alteration and climate change. For instance, desiccation events were shown to reduce functional diversity in stream biofilms, but rewetting by rainfall was sufficient to reset the functional diversity [67]. This ability to respond rapidly to rewetting might be crucial to sustain ecosystem functioning of biofilms in intermittent streams [67]. However, differential effects of desiccation on the autotrophic and heterotrophic processes in biofilms suggested that increased flow intermittency will increase the relative importance of heterotrophic processes in streams and also shift processing from the benthic towards the hyporheic zone [68]. Increasing temperatures were shown to have differential impacts on biofilm functional diversity. Warming of stream water by 3°C was found to increase functional diversity in stream biofilms, mainly due to a wider use of carbohydrates and polymers [69]. In contrast, an experimental study on stream biofilms showed a decrease in functional diversity under elevated (2°C) water temperature towards a specialized use of a few carbohydrates when grown under light, but a slight increase in functional diversity when grown under dark conditions [23]. This study also found that young biofilms were less affected by warming and less specialized in organic carbon use than mature biofilms, which suggests that the capacity to use a wide range of organic compounds might be advantageous for species pioneering biofilm formation [23].

Future perspectives

The rapid development of novel technologies in the last decades has pushed the limits to which the diversity of microbial communities can be explored, and provided the tools to unravel the mechanisms underlying the pattern of this diversity. However, theoretical and conceptual

approaches are needed as much as technical advances to integrate microbes into ecological research [70]. The application of ecological theory, such as landscape ecology, has greatly contributed to our understanding of microbial biofilms and can provide mechanistic insight into the causes and consequences of biofilm biodiversity [13,70]. Additionally, experimental studies are necessary to test causal hypotheses generated on the basis of the accumulating molecular data. Experimental systems, ranging from flow-cells to large stream mesocosms, have a long history in biofilm research and have led to major advances in this area [13,30]. Hypothesis-driven research and experimental validation of ecological theory have the potential to identify causal ecological relationships and to predict the responses of biofilm microbiota to a changing environment. Such knowledge is crucial if we are to understand the structure and functioning of natural microbial biofilms and the ecosystem services they provide.

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Figure 1. Schematic overview of the interplay of regional and local processes shaping biofilm diversity and community composition patterns. At the regional scale, hydrologic flow paths determine stream biogeochemistry and the metacommunity collected and transported by the streamwater. At the local scale, streambed topography and hydrodynamic conditions control turbulent transport of microbial cells and substrates to the surface, thereby affecting both dispersal and local environmental conditions. Biotic interactions like competition or protozoan grazing, for instance, further modify biofilm community composition and diversity.

Table 1. Some environmental factors potentially driving biofilm community composition and biodiversity in different habitats.

Environmental parameter	Community parameters affected	Habitat type	Reference
water temperature	bacterial community structure	benthic (epilithic and epipsammic), hyporheic, experimental	[21,23,24,27,36,42–46]
	bacterial and algal diversity	benthic (epilithic and epipsammic)	[41]
pH	bacterial community structure	benthic (epilithic and epipsammic), hyporheic, fine benthic organic matter	[12,21,22,28,36,43,47]
	bacterial diversity	benthic (epilithic), leaf litter	[22,33]
	fungal community structure	leaf litter	[33]
inorganic nutrients	bacterial community structure	benthic (epilithic), leaf litter, experimental	[19,33,42]
	bacterial diversity	benthic (epilithic)	[48,50]
	fungal community structure	leaf litter	[33]
	algal community structure	experimental	[19]
dissolved organic carbon	bacterial community structure	benthic (epilithic and epipsammic), hyporheic, aquifer	[12,27,52,53]
	microbial (bacterial and archaeal) diversity	aquifer	[52]

Glossary

Benthic zone: the interface between surface water and streambed sediment [8].

Complementarity: a mechanism underlying the diversity-function relationship based on local deterministic processes, such as facilitation and niche partitioning, which increases the performance of communities above that expected from the performance of the individual species [15].

Epilithic biofilm: a biofilm attached to stones or rocks [12].

Epiphytic biofilm: a biofilm attached to submerged plants [10].

Epipsammic biofilm: a biofilm attached to sand grains [8].

Epixylic biofilm: a biofilm attached to submerged wood [3].

Facilitation: any positive interaction between species, which benefits at least one of the participants and harms neither (such as increasing the availability of a limiting resource) [14].

Functional redundancy: the level of overlap in the functional capacities among the taxa of a community [59].

Hyporheic zone: the transitional zone located inside the riverbed sediment where surface water and groundwater mix [6].

Metacommunity: a set of local communities of potentially interacting species linked by dispersal [34]

Metabolic plasticity: the capacity of a community to accommodate environmental changes by adjusting the metabolic performance of present taxa [59]

Niche partitioning: to the process by which natural selection drives species into different uses of resources, thereby reducing interspecific competition [13]

Sampling effect/Selection effect: a mechanism underlying the diversity-function relationship based on stochastic processes involved in community assembly. More diverse communities have a higher probability of containing and becoming dominated by highly productive species, which means that diverse communities outperform the average but not the best performing species [15,63].